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Dynamic carbon allocation and the implication for
predicting response to fertilization

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Dynamic Carbon Allocation and the Implication for Predicting Response to Fertilization

Final

US Forest Service

Dynamic Carbon Allocation and the Implication for Predicting Response to Fertilization

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Summary

'Dynamic carbon allocation' refers to the hypothesis that resource allocation within individual plants is continuously adapted to changing circumstances rather than fixed throughout the life of the plant. The growth rate of above-ground plant components is often observed to increase in response to soil fertilization, and there is increasing evidence that this growth response is partly attributable to reduced carbon allocation to belowground components. Improved understanding of the allocation response to fertilization is needed both for the prediction of forest management impacts and to predict plant response to global environmental change. Study of the allocation response to fertilization, however, is complicated by the fact that dynamic root allocation may depend on many variables in addition to soil nutrient levels (e.g., the availability of water and organic carbon, species of plant, plant developmental stage, season of year, allometric relationships, root and mycorrhizae respiration rates, and fine root turnover rates). Moreover, both positive and negative interactions may occur between many of these variables.

The results of this study suggest that at present no ecosystem simulation models exist which successfully incorporate simulation of C allocation responses to changes in nutrient availability and which can be calibrated with ecosystem data. Understanding and simulating dynamic C allocation remains a major pre-requisite to predicting growth response to fertilization. Data compiled through the Intermountain Forest Tree Nutrition Cooperative could be used in the future to explore possible changes in C allocation in response to fertilization. Belowground production and allocation changes are not readily measured, however, and are not included in the available data. Several analytical steps are required to calculate belowground allocation as the difference between total C production and aboveground utilization for respiration and growth. No ecosystem models calibrated for the Intermountain region appear to be available with which to calculate total photosynthate production, aboveground growth and respiration. In the near future empirical modeling approaches may therefore have to be considered as an alternative approach to predicting fertilization response.

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Table of Contents

Summary	i
Acknowledgments	ii
1.0 Introduction	1
2.0 Empirical Evidence for Dynamic Carbon Allocation	1
3.0 Importance of Varying Root Allocation	2
4.0 Factors Expected to Influence Carbon Allocation to Roots	3
5.0 Fertilization Effects on Plant Growth	4
6.0 Existing Root Allocation Models	6
6.1 Empirical Models	6
6.2 Functional Models	6
6.3 Mechanistic Models	10
6.4 Combination Models	11
6.5 Other Models	11
7.0 Implications for the IFTNC	13
8.0 Literature Cited	14
Appendix 1: Related Literature Not Cited in this Report	20
Appendix 2: Summaries of Some Ecosystem Models without Dynamic C Allocation	26
Appendix 3: Potential IFTNC Carbon Allocation Analysis	30

List of Tables

Table

6.1 Input requirements, computational methods, and output results of existing carbon allocation models	7
6.2 Suitability of some existing allocation models for predicting stand fertilization response.	13

1.0 Introduction

Tree growth is often limited by a scarcity of nitrogen (N) in the coniferous forests of western North America. In many cases, these forests show increased growth in response to N fertilization. The three mechanisms usually proposed to account for this response are:

1. an increase in foliage biomass and leaf area, allowing plants to intercept more solar radiation;
2. an increase in foliage nitrogen levels, which increases the efficiency of photosynthesis; and
3. a decrease in the proportion of new photosynthate that is allocated to fine roots, which would allow plants to invest more in both foliage and stem growth.

The first two mechanisms of fertilization response have long been well-supported (e.g., Brix 1992). The third mechanism is known as the “dynamic carbon allocation” hypothesis, because of the suggestion that resource allocation within the plant is continuously adapted to changing circumstances rather than fixed throughout the life of the plant. Although clearly “controls on allocation are a major component of a plant’s overall adaptive ‘strategy’ ” (Shaver and Aber 1996), an allocation response to fertilization has not been well supported by the literature until recently (Haynes and Gower 1995). The following sections of this report discuss the empirical evidence for dynamic carbon allocation, and its significance to efforts to project stand dynamics. The range of factors expected to influence root allocation is discussed, as is the range of fertilization effects on plant growth. Existing root allocation models are then described. A final section of the report considers the implications of work in this area to the Intermountain Forest Tree Nutrition Cooperative. The appendices contain a listing of related literature that is not directly cited in this report, summaries of ecosystem models without dynamic C allocation, and a discussion of a potential approach to analysis of IFTNC data that addresses C allocation changes.

2.0 Empirical Evidence for Dynamic Carbon Allocation

Dynamic carbon allocation theory predicts that plant allocation between aboveground and belowground components should favor the parts most limiting to growth. Thus plants growing on nutrient poor sites are expected to allocate a larger proportion of available resources to roots, all else being equal. Measuring this response, however, is complicated by seasonal, annual and spatial variation in the observed foliage:root ratio and in resource availability (see discussion in Kurz 1989b).

Scientific interest in the area was stimulated by the observations made by Keyes and Grier (1981) of 40-year old Douglas-fir on different quality sites. These authors found that the net primary production of Douglas-fir was only slightly higher on good than bad sites (17.8 tons/ha vs. 15.4 tons/ha), but that twice as much carbon is allocated to roots on poor sites. They concluded that the greater aboveground growth observed on good sites was largely because of differences in allocation. Kurz (1989b) measured fine root density in coastal Douglas-fir and also found a greater density of fine roots on poor sites. Within those sites, however, root density was greatest on the better parts of each site. This supports the idea that roots preferentially invade good micro-sites and/or live longer on good micro-sites.

As reviewed in Hendricks et al. (1993), a number of experimental studies since Keyes and Grier’s paper have reported that fertilization decreased fine root production or fine root biomass, but just as many studies have reported fine root biomass increased following fertilizer application. Hendricks et al. suggest that this variation between studies arises from variation in tree species and age, the fertilization treatment applied, assessment

methodology, and most importantly the timing of assessment post-treatment (see also Ericsson 1990). These authors also conduct a nitrogen budget assessment of the data presented by Keyes and Grier, and find that the reported data actually suggest that trees on the poor-quality sites had to uptake a larger quantity of nitrogen (N) than trees on high-quality sites in order to support their greater density of roots (which are relatively nitrogen rich compared to other parts of the plant). Since this seems unlikely, Hendricks et al. conclude that the maximum-minimum soil-core methods employed by Keyes and Grier probably under-estimated root production on the rich site. This sampling method is insensitive to variation in root turnover rate. Sequential core estimates of fine root production can sometimes exceed estimates of *total* root carbon allocation (Hendricks et al. 1993). Burke and Raynal (1994) found that estimates of fine root production obtained by three different methods differed as much as 50% from one another.

The largest growth responses to N fertilization that Thomas and Mead (1992) observed in radiata pine were belowground, with total root biomass of fertilized trees being up to 55% higher than that of controls. As the authors note, root:shoot ratio appeared to increase with tree size on the control plots as well, so the increased root biomass of fertilized trees could be a result of their increased total size. When this allometric effect was taken into account, there was no remaining significant effect of fertilization on root biomass. Moreover, the greater observed root biomass of fertilized trees could partly reflect the result of decreased root turnover rates.

Some of the clearest evidence to date of a shift in root allocation in response to fertilization is provided by Haynes and Gower 1995. They used two independent analysis methods to show that fertilization decreased both fine and coarse root production in red pine plantations in northern Wisconsin. Aboveground production was significantly increased by fertilization in this study, so that all fertilized plots were observed to have a lower proportion of carbon allocated belowground. An earlier experimental study found that fine root production decreased in a Douglas-fir forest in New Mexico as nutrient availability was increased (Gower et al. 1992).

The earlier scarcity of data supporting an allocation response to fertilization may reflect the difficulty of obtaining measurements of root production rather than a lack of generality of such a response.

3.0 Importance of Varying Root Allocation

Gillespie and Chaney (1989) found in their review that “a large proportion of the stem growth that occurs in response to fertilization can be attributed to increase leaf area” and an increase in photosynthetic efficiency. These factors on their own, however, appear to be insufficient to explain the magnitude of the observed above-ground growth response. Changes in photosynthate allocation to roots are therefore considered as an additional factor.

The issue of dynamic allocation is important to predicting plant growth responses to global atmospheric change. For example, Kirschbaum et al. (1994) compared the effect on growth projections of either holding root allocation constant or allowing it to increase towards the empirically observed maximum as foliar nitrogen levels decreased. They found that the increase in wood production expected from a doubling of atmospheric CO₂ concentration was reduced by 25% when root allocation was assumed to vary with foliar nitrogen.

Under climate change scenarios, the balance between forest production rates and decomposition rates will likely depend on whether plants can access sufficient nutrients to support increased production rates. As stated by McMurtrie and Wang (1993), “ecosystem models rigorously integrating carbon and nutrient cycles are urgently required to estimate growth rates which can be maintained at elevated [CO₂ levels] by vegetation in nutrient-limited environments.”

4.0 Factors Expected to Influence Carbon Allocation to Roots

As listed below, plant carbon allocation to roots is expected to depend on numerous factors of which resource availability is only one:

1. Allometric relationships, which determine for example the amount of fine root mass required to support a given leaf mass or the amount of total root mass required to provide the structural support for the aboveground biomass. For example, coarse root biomass is closely related to aboveground biomass (Haynes and Gower 1995, Kurz et al. 1996).
2. The mortality rate of fine roots. As reported by Burke and Raynal (1994), fine root turnover in northern hardwoods is on the order of 100% per year. Because of the relatively high turnover rate of fine roots, fine root production accounts for a larger proportion of total production than would be expected from its biomass alone. Fine-root lifespan depends on site quality, the occurrence of drought or flooding, etc. In their review of available data, Hendricks et al. (1993) show that the turnover rate of fine roots is greater on sites with higher nitrogen availability. This may occur as a result of fine roots on rich sites having higher rates of metabolic activity and more quickly consuming the energy stores allocated to them during root formation (see Hendricks et al. 1993). Note that variation in root density may arise from either differential root production rates or different root lifespan (see Shaver and Aber 1996 for further discussion).
3. Season of year.
4. Plant developmental stage.
5. Root and mycorrhizae respiration rates, which will depend on temperature and nutrient uptake activity.
6. Plant species. Not only does potential growth rate vary with species, but different species appear to adopt different biomass nutrient concentrations when grown on the same initial soil conditions, and these differences feed back on soil nutrient levels (Eriksson and Rosen 1994). Laurence et al. (1994) found that species with high relative growth rates more readily change their allocation patterns in response to stress. Similarly, Salomonson et al. (1992) found that the less toxic of two perennial forest herbs was better able to adjust growth and nutrient allocation patterns in response to different levels of potassium availability.

An important factor in root allocation that has not always been acknowledged is the intensity of individual competition for which the plant species is adapted. King (1993) showed that the root:foliage allocation strategies that maximized wood production were quite different when the analysis considered the wood production of an individual focal tree within a stand rather than the total wood production of an entire stand. At any specified level of soil N, stand wood production is maximized at a 'cooperative' optimum where the allocation to roots is relatively low. An individual plant within this stand, however, could obtain greater wood production by investing more in roots than its neighbors and hence out competing those neighbors in the quest to obtain nutrients. Over evolutionary time, this advantage is expected to have lead to the "competitive" optimum at which all individuals invest more heavily in roots than would be expected from the goal of maximizing stand production. In King's analysis, the result is that total stand wood production at the competitive optimum is only 54% of that for a stand at the cooperative optimum.

7. The availability of resources (N, water, total C). As discussed below, this will depend on vegetation abundance, fertilization treatment and many other factors some of which lead to a complex series of interactions.

Shafii et al. (1990) presented an empirical model and independent data which both showed that trees in low density stands respond more to fertilization than trees in higher density stands, presumably because the latter trees are experiencing relatively greater light limitation. There is an interaction between density and nutrient availability because canopy closure slows the rate of decomposition and mineralization (Waring 1987). Dynamic allocation may itself feed back on nutrient availability, since a decrease in fine root density will reduce the efficiency of nutrient uptake from the soil and allow more nutrients to be lost through leaching. This may be one of the factors that limits the observed fertilization response post-treatment—as soil N returns to background levels, trees may be left with less fine root mass than before with which to capture remaining N. As noted by King (1993), “although collective, short-term stand wood production can be increased by shifting growth from roots to stems, this strategy may increase nutrient losses, ultimately decreasing productivity.”

Another expected interaction is that between site moisture levels and N availability, since moisture levels influence the rates of decomposition, mineralization, and ion transport (Grier et al. 1986). Moreover, as Waring (1987) noted, drought forces roots to extract water from deeper soils, where fewer nutrients are available. Field et al. (1992) note that the effect of fertilization in increasing photosynthetic efficiency is greater under dry conditions.

Generally, the most efficient allocation of resources to different tissues is that which results in growth being equally limited by all resources (Chapin et al. 1987). Gleeson and Tilman (1992) in their ‘multiple limitation hypothesis’ arrive at a similar conclusion from their consideration of optimal foraging theory: plants should be “adjusted” to make all resources simultaneously limiting. Note that this does not mean resource enrichments of every nutrient will produce equally strong growth responses (Gleeson and Tilman 1992). Rather a detectable response will be seen only for enrichment of those nutrients that have been costly for the plant to acquire in the absence of enrichment. No response at all is expected for resources that are acquired in excess as a simple by-product of “simultaneous uptake”. Many resources may be acquired simultaneously through allocation to a single structure so that enrichment of one of these resources does not release the plant from the need to invest in this structure. As Gleeson and Tilman show, these considerations mean that diminishing returns are expected from successive increases in a single resource, but that highly non-additive returns may be obtained from simultaneous increases in two resources. Plants that are adapted to rapidly-changing environments, however, are not expected to produce large vegetative structures in response to an increase in environmental quality (Iwasa 1991). This is because, in a highly changeable environment, the increase in quality is not likely to last long enough for the plant to recover their investment in the new structure.

Robinson (1994) reviewed 49 studies that varied the spatial concentration of N, P, and K available to the root systems of individual plants. In the majority of these studies, individual root systems responded in the expected manner to spatial variation in nutrient concentration. That is, root growth was greater in nutrient rich patches and less elsewhere when compared to the root growth of plants in a uniformly rich environment. Plants growing in non-uniform environments (partly nutrient rich and partly nutrient poor) generally had a greater total root:shoot ratio than plants in the uniformly rich environments, although many studies found no significant change in the root:shoot ratio. As Robinson suggests, the lack of change in these studies may be because the nutrient in variable supply was not limiting to plant growth.

5.0 Fertilization Effects on Plant Growth

The effects of N-fertilization on plant growth include increased leaf area, leaf nitrogen, photosynthetic efficiency, and stem growth, and reduced root mortality (see Gower et al. 1992; Burke et al. 1991; Mika and Vander Ploeg 1991; Colbert et al. 1990; Gillespie and Chaney 1989). Grier et al. (1986) found that fertilization with N, P and S all increased the growth of Douglas-fir with the largest growth response seen on the poorest sites. They also

observed an increase in leaf area at a given basal area (through an increase in needle size, the number of needles per shoot, and the number of current shoots), and an increase in the net photosynthetic production per unit of leaf area. Shafii et al. (1989) found that basal area and height growth of Douglas-fir and grand fir were increased over 6 years after treatment with N fertilizer. Fourteen years after treatment, volume was 14% higher on unthinned fertilized stands than on control stands, and 23% higher on thinned fertilized stands.

Both positive and negative mechanisms have been proposed to reinforce these growth effects. Increased energy availability (in the form of organic C) following fertilization may increase the rate of N uptake by roots (see Johnson 1985). However, the rate of nutrient uptake per unit of root may be decreased when nitrogen availability is increased (Field et al. 1992).

Another effect of fertilization is that the optimal tissue N concentration is increased (Gleeson 1993). This may create a pressure to maintain allocation to roots more than might otherwise be anticipated. However, combined with the fact that fertilization reduces the resorption of nutrients from senescent tissues (Field et al. 1992), the resulting increase in N:C ratio in leaf litter increases the mineralization rate (see Gillespie and Chaney 1989). This will tend to sustain the increased N availability as a result of fertilization (see also Shaver and Aber 1996 and references therein).

Increasing N availability may also have some less intuitive effects. For example, fertilization has been observed to reduce the concentration of C-based metabolites (e.g. lignin, terpenes, tannins) that act to protect the plant from predators (Field et al. 1992). It appears that as the C:N ratio falls in the plant, C is increasingly allocated to growth instead of these defensive compounds. This is consistent with the observation that drought can increase plant stores of carbohydrates and defensive compounds in the short-term because it immediately reduces shoot growth (see Waring 1987). Fertilized sugar maple begin storing starch later in the season and store less total starch than do unfertilized plants (Burke et al 1991). The lower starch:sugar ratio in the fine roots of fertilized plants is consistent with their greater susceptibility to frost and pathogens, since frost hardening is mainly accomplished with the products of starch digestion (Burke et al. 1991).

Moreover, fertilization may alter the nutritional balance of the plant. By promoting increased growth, an excess of one nutrient may lead to relative deficiencies of other nutrients (Waring 1987). There is experimental evidence that such a process leads to increased root rot damage in white pine seedlings (see Waring 1987). Burke et al. (1991) found that the ratio of organic sulphur to nitrogen was greater when sugar maple grow under nitrogen deprivation, suggesting that more sulphur-containing proteins are produced when N availability is low. Mika and Moore (1990/91) found that potassium status appeared to limit interior Douglas-fir response to N fertilization, with stands with low potassium levels showing less response. Yellow and necrotic shoot-tip symptoms in white spruce and Engelmann spruce were associated with low needle potassium concentrations, and these symptoms are made worse by N fertilization (van den Driessche and Ponsford 1995). Scots pine seedlings given greater amounts of N suffered greater damage when inoculated with a pathogen that causes scleroderris canker (Ylimartimo 1990/91). Similar effects of N availability could be seen when pathogen mycelium was grown in artificial media—mycelial growth was reduced by increases in the concentrations of potassium and calcium, but this growth was increased by a modest increase in the concentration of nitrogen (Ylimartimo and Haansuu 1993).

Mika and Vander Ploeg (1991) and Moore et al. (1991) analyzed interior Douglas-fir fertilization data from 94 sites in 6 geographic regions, and noted that fertilized plots had greater mortality rates post-treatment than control plots. In fact, the increase in mortality was such that only in two regions did fertilization increase net basal area and volume growth (although gross basal area and volume growth were increased by treatment in all regions). The increase in mortality was also greater at higher fertilization treatment levels, in spite of the fact that the highest treatment level was required to bring foliar N to levels considered adequate. The mortality factors involved included wind, snow, root rot and bark beetles. The increased mortality appears to be greater than would be expected from increased competition due to accelerated growth, and so may provide evidence of the importance of nutritional balance or decreased allocation to defense during rapid growth.

By increasing foliage growth and hence water demand, N fertilization may also make trees less drought resistant. Nilsen (1995) found that fertilized Norway spruce trees suffered more under experimentally induced drought. Higher water consumption in the fertilized trees lead to significantly lower pre-dawn shoot water potential, and there were clear effects on photosynthesis. The resulting decrease in growth was most pronounced at higher levels of fertilization. An index of water strain suggested that drought-induced stress was positively correlated with needle biomass.

6.0 Existing Root Allocation Models

Existing root allocation models may be broadly classified as empirical, functional, mechanistic, or a blend of these types. This section discusses in general terms some of the existing models in each class and considers their suitability for predicting fertilization response. A more numerical description of some of these models, along with a summary of their input requirements, may be found in Table 6.1 below. Some ecosystem carbon models that lack dynamic allocation are described in Appendix 2.

6.1 Empirical Models

Empirical models are developed by fitting equations to the observed phenomenon. Probably the majority of existing plant allocation models use empirical allometric coefficients to control partitioning (e.g. Aber et al. 1994a; Aber and Federer 1992; Korol et al. 1991; Webb 1991; the AIRPTAEDA and SILVA models described in Kiester et al. 1990; Burk et al. 1990; Sievanen and Ek 1988; see other references in Gillespie and Chaney 1989). Generally, these models employ constant coefficients so that the proportional allocation of photosynthate is also constant.

6.2 Functional Models

“Functional” models are those that attempt to predict allocation by considering the function of each tissue type, and the overall goals of the plant.

Under “uptake balance” models, for example, a constant “optimal” ratio is maintained between total root absorption and total plant photosynthesis (Davidson 1969; Garnier 1991). Gleeson’s analysis (1993) of an uptake balance model and a number of variants of it showed that the optimal leaf nitrogen concentration is an increasing function of soil nitrogen availability under a range of conditions: no cases were found where tissue N did not respond to soil N if it was permitted to vary in the model. In most biologically-probable situations, root allocation is expected to decrease in the model as tissue nitrogen increases in response to an increase in soil nitrogen. However, the predicted decrease in root allocation is less than is expected when tissue N is assumed to remain constant independently of soil N. In his exploration of the model, Gleeson shows that accounting for the respiration cost of roots leads to an increase in shoot allocation.

Note that uptake balance models on their own consider only allocation to foliage and roots, and do not attempt to predict allocation to stem tissue, defensive compounds, or reproduction (Shaver and Aber 1996). Moreover, the truly “optimal” allocation in particular circumstances is not necessarily a balanced one as any excess uptake or production of a resource may be stored as a hedge against future uncertainty or respired (Gleeson 1993). More realistically, long-term survival would take precedence over short-term production gains wherever there were a trade-off between the two in long-lived plants such as forest trees.

Table 6.1: Input requirements, computational methods, and output results of existing carbon allocation models. Abbreviations used are as follows: C for carbon, N for nitrogen, L for leaves, S for “stem” (including branches and coarse roots), and R for fine roots.

Input	Methods	Output
Transport Resistance Thornley 1972, 1991 (as implemented in Rastetter et al. 1991) Pre-allocation concentration of labile C and N in L, S, and R. Total stem structural carbon. Stem conductivity parameter. C transport parameter for L:S and S:R. N transport parameter for R:S and S:L. [for growth calculation: growth efficiency parameters, maximum growth rates, “C to N range” parameters, and “non-restricted C/N ratio” parameters for L, S, and R; and a growth temperature-response function.]	The transport of labile C and N between L, S, and R is estimated. The growth of each tissue is a temperature-dependent function of the resulting concentration of labile C and N in each tissue. The transport of C from L to S to R depends on the initial difference in labile C concentration between the donor and recipient tissues, stem size, a stem conductivity parameter, and a C transport parameter specific to each donor:recipient pair. The transport of N in the opposite direction is calculated in the same manner using labile N concentrations and N transport parameters. Labile C and N concentrations in each tissue are calculated as the ratio of total labile C or N in that tissue to total structural C in that tissue.	Post-allocation concentration of C and N in L, S, and R. New growth of L, S, and R.
As described for Rastetter et al. except that additional parameters are required to treat branches and coarse roots as separate tissues.	Transport Resistance (as in Thornley 1991) Essentially as summarized above for Rastetter et al (1991) except that branches and coarse roots are treated separately from stem wood, and that the conductances of these tissues are calculated considering the amount of meristem tissue alone.	Post-allocation concentration of C and N in L, R, branches, stem, and coarse roots. New growth of each of these plant components.

Table 6.1: (continued)

Input	Methods	Output
Total photosynthate production, N uptake, and leaf N translocation. 'Hydraulic resistance' to C and N transport for each of L, sapwood, and R tissues, and of stem sections between each tissue pool. 'Hydraulic pressure' of C and N in each of L, sapwood, and R tissues, which is a function of C:N ratio in each tissue.	Mass Transport Fernandes et al. 1996 Uses an electrical analog model to calculate C and N transport to each tissue, assuming that nutrient fluxes can be modeled like electrical current with photosynthate entering the electrical circuit from the foliage and N entering from both root uptake and leaf translocation. The 'hydraulic resistance' to movement of each resource in the circuit is associated with the cross-sectional area of 'pipes' provided for movement, and hence decreases with the total biomass of each tissue. The 'hydraulic pressure' of each tissue is inversely related to its sink strength, with current expected to flow from high to low pressure tissues depending on the pressure difference between each pair of tissues. Note that Fernandes et al. were able to calibrate the model to actual experimental stand data by varying some parameters (including all 10 of the resistance parameters) and deriving others through analytical relationships to available data. No labile resource pools need be estimated under this allocation scheme.	Post-allocation biomass of L, R, sapwood and heartwood. Post-allocation ratio of C:N in each tissue.
Total N in plant tissue and total plant biomass. Rate of photosynthetic production per unit of shoot biomass, as a function of plant N. Rate of N uptake per unit of root biomass, as a function of N availability.	Uptake Balance Davidson 1969, Gleeson 1993 Assumes that the ratio of total shoot photosynthetic production to total root absorption is constant. From this it follows that (see Gleeson 1993), at balanced growth, the ratio of R:S must be the same as the ratio of i) the product of plant N concentration and photosynthetic rate per unit of shoot, to ii) the rate of N uptake per unit of root. Gleeson 1993 extends this basic model to incorporate joint optimization of tissue N levels and R:S allocation.	Expected R:S ratio.

Table 6.1: (continued)

Input	Methods	Output
Density of C and N available 'in the environment.' 'Capture rates' of C and N per unit of resource in the environment per unit expenditure. Demand ratio of C:N required for plant growth.	Multiple Resource Limitation Gleeson and Tilman 1992 Deduces from optimal foraging theory that growth rate will be maximized by the 'diet' (i.e., rates of C and N uptake) in which both C and N uptake are simultaneously limiting. This holds for any given set of maximum attainable C and N uptake combinations. If linear consumption constraints are assumed, the optimal ratio of allocation to C acquisition to that of N acquisition is proportional to the ratio of i) the product of carbon resource density in the environment and the 'capture rate' of C per unit environmental C per unit expenditure, to ii) the product of N resource density in the environment and N capture rate. The constant of proportionality is the demand ratio of C:N required for plant growth.	Optimal proportion of total 'uptake expenditure' that should be allocated to acquisition of N vs. C.

Another balance model is that developed by Johnson (1985) in which root:shoot growth is prioritized based on the ratio of total substrate carbon to total nitrogen in the plant. Johnson proposed as a hypothesis that this ratio should remain in a constant proportion to the ratio of shoot weight to root weight during “balanced exponential growth”. Partitioning in this model depends on the state of the plant, and not on resource uptake rates which must be incorporated in the empirical constant of proportionality (which is dimensionless). In the simple form proposed, this model cannot account for increased shoot nitrogen levels in response to increased soil nitrogen availability, or the resulting effects on photosynthetic efficiency.

King’s simulation model (1993) determines the foliage and root allocation required to maximize wood production. The modeling scheme used could be characterized as “nitrogen loss replacement”. It assumes that the change in woody tissue N is equal to the amount of N remaining after root uptake is used to replace the N lost through litterfall and root death. King then determined the consequence for wood production of a range of root and foliage biomass allocation patterns.

Ågren and Wikström (1993) provide a good review of models with an explicitly evolutionary approach. These models are not considered further here because they are difficult to apply to plants such as trees that are long-lived with reproductive biomass constituting only a very small proportion of total biomass.

6.3 Mechanistic Models

“Mechanistic” models are based on explicit processes of plant growth, with the hope that realistic modeling will make the model exhibit the observed phenomena.

The scope for mechanistic models of plant carbon allocation is limited primarily by a lack of knowledge of the mechanisms controlling partitioning (Gillespie and Chaney 1989). “Transport resistance” models, however, have formed a very successful class of mechanistic models. In transport resistance models (Thornley 1972, 1991; also implemented in Thornley and Cannell 1992, and Rastetter et al.’s 1991 “General Ecosystem” model GEM), root allocation is calculated by assuming that the transport of C and N between the roots and the foliage is a function of concentration gradients within the plant. The growth rate of each tissue is assumed to be proportional to the concentrations of C and N in that tissue. As explained by Shaver and Aber (1996), the effect in these models is that:

...roots and shoots compete for labile carbon and nutrient substrates to support growth, with roots having the advantage with respect to nutrient supply and shoots with respect to carbon supply. The result is that root growth is favored over shoot growth when nutrient supply is low, and shoot growth is favored over root growth when carbon supply is low.

These models have performed well in reproducing observed allocation responses. Wilson (1988) concluded from his review that Thornley’s transport resistance model was more parsimonious than function equilibrium models, and more compatible than allometric models with the available evidence on plant responses. However, transport resistance models have been criticized on numerous grounds. These models typically assume that soil nutrient levels are constant, independent of the rate of absorption by roots (Shaver and Aber 1996). They also assume that the photosynthetic rate of leaf tissue is independent of nutrient content (Wilson 1988). Furthermore, as described by Fernandes et al. (1996), the labile C and N pools in transport resistance models “do not correspond directly with measurable quantities, and ... make the model difficult to calibrate”; the sizes of these pools evolve rapidly in the models “and so are computationally intensive to model numerically”; and can exhibit “unstable behavior for aggrading systems” due to weak coupling between labile and structural pools for the non-limiting resource.

Finally, a general weakness of the models is that N is not transported within the plant by the same diffusion-like mechanism as is C (Dewar 1993). N is transported from root to shoot primarily through the xylem by mass flow

driven by transpiration (rather than the N concentration gradient), and is then transported to the sites of growth or storage by translocation through the phloem. In white lupin, in fact, much of the N used in root growth is obtained from the shoot and most of the rest is obtained from transfer between xylem and phloem, with very little direct N transfer between root uptake sites and root growth sites (see references in Dewar 1993). A more realistic model of N transport could potentially produce more robust predictions under a wider range of conditions. Dewar's model (1993) is an attempt to refine Thornley's basic model of C transport and local tissue growth by incorporating an improved model of N transport. The model developed by Fernandes et al. (1996) for GEM is also an adaptation of Thornley's model that preserves the C- and N-dependent local tissue growth while substituting a more elaborate model of resource transport based on mass transport or pressure flow.

6.4 Combination Models

The TREGRO model described in Kiester et al. (1990) and implemented in the ROPIS-WEINSTEIN computer model uses a combination of mechanistic and functional approaches. In this model, new tissue is only constructed in each component of the plant (4 classes of leaf, branches, stem, fine roots and coarse roots) if all the necessary C and nutrients are available in that plant part to maintain required stoichiometric relationships. High priority components of the plant have the first opportunity to use available C; if these components are lacking in the nutrients required to build new tissue, the available C is passed on to the next priority component. The priorities assigned to different tissues depend upon the phenological condition of the tree, and also vary depending on 7 different seasonal periods. When tested against data from a field experiment on red spruce, the model was found to be "capable of predicting total weight gain within 2% and weight gain of various tissues within 10%."

The ROPIS-CHEN model (Kiester et al. 1990) is another hybrid model. In this model, the maximum possible growth of canopy and roots are derived from empirical allometric relationships, but whether or not the maximum growth potential of each tissue is achieved depends on nutrient status. Due to the complexity of the complete model, the model developers chose to evaluate the model through a series of 8 workshops with plant physiologists. Most of the participants are described as having been "supportive" of the model as a whole. The allocation algorithm appears not to have been evaluated separately.

6.5 Other Models

"Pipe models", like that employed by Mäkelä (1986) are based on water transport resistance, where the sapwood is viewed as an assemblage of pipes connecting plant foliage to roots. Pipe models assume that the cross-sectional area of sapwood at any height is proportional to the foliage area above that point. Foliage growth then requires increased sapwood biomass with an associated increase in production and maintenance costs. Note that pipe model theory itself determines only the ratio of sapwood to foliage—the growth of fine roots must be predicted by some other means (e.g. functional balance in the case of Sievanen 1993 and Mäkelä 1986, 1987, and submitted; see also Mäkelä 1990, and Ågren and Wikström 1993). Pipe models have been criticized because the area of sapwood tapers between the base of the tree and the bottom of the live crown, and the sapwood:foliage relationship changes further within the crown (Kiester et al. 1990). As noted by Ågren and Wikström (1993), a major consequence of pipe model theory is that "the height growth of the tree increases the length of the pipes and every new pipe that is produced and connected to the top of the tree will therefore be more costly in production and maintenance than those lost when the lower part of the canopy dies.

A review of other components of 7 different ecosystem models (BIOMASS, BIOME-BGC, CENTURY, MBL-GEM HYBRID PnET-CN, and Q), not all of which have N-dependent allocation, may be found in Ryan et al. (1996). Components of the BIOMASS and MAESTRO models are compared in McMurtrie and Wang (1993), although carbon allocation is not discussed in this paper.

6.6 Suitability of Existing Models For Predicting Fertilization Response

To be suitable for the prediction of stand fertilization response, a model must allow root:shoot allocation to vary with tissue N levels *and* be fit to real-world stand and site data. Table 6.2 below lists existing quantitative growth models and indicates whether each model meets these criteria. As suggested by the table, some models may have elegant theoretical solutions but their calibration requires parameters which are not readily obtained by field experiments. Other models that have managed to incorporate experimental data tend to be more limited in their representation of dynamic carbon allocation.

As a general caveat, note that all of these models assume one constant rate of nitrogen uptake for the entire root system of each plant. That is, none of the models deal with spatial variation in nutrient availability or root density within the level of an individual root system.

Note too that all of the models that are sufficiently complex and realistic enough to be fit to real-world stand and site data also have a great many “degrees of freedom” due to the great many parameters that must be calibrated. That is, there is a danger that the large number of free parameters may permit the models to be fit well to relatively small sets of experimental observations, regardless of whether the modeling concepts have managed to capture the important dynamics of the system. The potential of model calibration to conceal weaknesses in model logic is apparent in Ryan et al.’s (1996) comparison of the projections of 7 different ecosystems models (BIOMASS, BIOME-BGC, CENTURY, MBL-GEM HYBRID PnET-CN, and Q). The carbon allocation schemes in these models range from constant percentages to allometric equations, pipe models, and transport resistance models. Modelers were given summary data for two diverse sites (one a coniferous site in Sweden and the other a radiata pine site in Australia) with which to calibrate and adjust their models. The models were then used to project stand development over a five-year period under different treatments. Several of the models closely predicted total stem biomass on both sites under both control and fertilization treatments. Yet the models accomplished this without accurately predicting foliage production, foliage nitrogen, or stem wood production under fertilization at either site! Clearly calibration efforts were focused on the net effect of the model, and not the performance of individual sub-models. Ryan et al. (1996) note that the models had particular difficulty allocating carbon and especially nitrogen within plants. In fact, when compared with the actual data, the models that used flexible allocation did not do noticeably better than the models with fixed allocation.

It is clear that a successful predictive model of plant response to fertilization must at a minimum incorporate photosynthetic rates that are dependent on leaf nitrogen levels, nitrogen uptake rates that are dependent on the amount of root carbon, and tissue allocation that is dependent on both nitrogen and organic carbon availability. Because of the number of possible interactions between water and nutrient availability, it may be that only a fully detailed ecosystem model could accurately predict the optimum fertilization and irrigation regime under different site conditions. For example, the rate of N uptake depends on the form of N available, the rate of water uptake, soil adsorption properties, and all the litter and site characteristics that affect the mineralization rate and amount of soil N (see discussion in Gillespie and Chaney 1989). Because of density-nutrient interactions, a successful predictive model may also have to account for the mortality of individual trees via competition, and not just the stand-average mortality implied by the balance between respiration and production—carbohydrate deficit is not the only cause of mortality (see Kiester et al. 1990).

Table 6.2: Suitability of some existing allocation models for predicting stand fertilization response. The table indicates whether root:shoot allocation is dependent on tissue N levels in each model, and whether the model has been fit to real-world stand and site data.

Authors	Title / Description	N-dependent root:shoot C allocation?	Fit to stand and site data?
Johnson 1985	balanced exponential growth	YES	NO
Weinstein & Beloin, reported in Kiester et al. 1990.	ROPIS-WEINSTEIN (TREGRO)	INDIRECT	YES
Iwasa 1991	optimal growth in stochastic environments	NO	NO
Garnier 1991	uptake balance	YES	NO
Rastetter et al. 1991; Fernandes et al. 1996	transport resistance (in GEM)	INDIRECT	YES
Running & Gower 1991	FOREST-BGC	NO	YES
Thornley 1991	transport resistance	YES	NO
Webb 1991	'carbon flow' growth model	NO	YES
Aber & Federer 1992; Aber et al. 1994a,b	PnET, PnET-II, PnET-Day	NO	YES
Gleeson & Tilman 1992	multiple resource limitation	YES	NO
Thornley & Cannell 1992	transport resistance + soil model	YES	NO
Gleeson 1993	uptake balance & optimisation of tissue N	YES	NO
King 1993	competitive optimisation of resource acquisition	YES	NO

7.0 Implications for the IFTNC

Forest fertilization experiments are implemented to increase the understanding of stand responses to nutrient additions. This understanding can then be used to develop predictive tools that assist in the selection of stands in which the greatest benefits are anticipated and in the design of treatment schedules aimed at meeting forest management objectives.

As discussed earlier in this report, nitrogen fertilization generally increases stand foliage biomass and, through higher N content of the foliage, increases foliage efficiency. Both factors contribute to greater photosynthate production. The photosynthate is utilized by above- and belowground stand components. Empirical studies suggest that the proportional allocation to belowground components decreases with greater nutrient availability (e.g., Haynes and Gower 1995). The observed aboveground response to fertilization thus depends in part on the change in photosynthate allocation between aboveground and belowground components. Understanding and

simulating dynamic C allocation is therefore a major pre-requisite to predicting growth response to fertilization.

The results of this study suggest that at present no ecosystem simulation models exist which successfully incorporate simulation of C allocation responses to changes in nutrient availability and which can be calibrated with ecosystem data. The predictive capability of existing models is limited by a lack of understanding of the mechanisms of C allocation.

In the absence of a suitable model, the question arises whether the data compiled through the Intermountain Forest Tree Nutrition Cooperative could be used to explore possible changes in C allocation in response to fertilization. Belowground production and allocation changes are not readily measured, however, and are not included in the available data. Several analytical steps are required to calculate belowground allocation as the difference between total C production and aboveground utilization for respiration and growth (as outlined in Appendix 3). To obtain the annual estimates of total photosynthate production and respiration, an appropriately calibrated ecosystem model could be used for each of the years following fertilization. No ecosystem models calibrated for the Intermountain region appear to be available with which to calculate these parameters.

In the near future, empirical modelling approaches will therefore remain the main alternative approach to predicting fertilization response.

In the medium term, a physiological model will be needed that can estimate annual total photosynthate production and respiration on a stand-by-stand basis. Combining this information with the data compiled by the IFTNC (as outlined in Appendix 3) could then be used to explore possible changes in C allocation in response to fertilization. Results from this analysis can then be used to develop preliminary parameters for simulating dynamic C allocation.

In the long term, an ecosystem-level model of forest dynamics that includes above and belowground processes and simulation of C allocation that is responsive to environmental conditions will be required to predict fertilization effects over the range of ecosystem types in the Intermountain Region.

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Appendix 2: Summaries of Some Ecosystem Models without Dynamic C Allocation

Model	Running and Gower 1991 'FOREST-BGC' extension
Summary	A new version of FOREST-BGC that allows carbon partitioning to depend on water and nitrogen availability.
Calibration	hypothetical coniferous stands in Wisconsin and Montana
Vegetation scale	models stand averages of the carbon and nitrogen concentration per hectare in leaves, stems and roots
Spatial representation	none
Time step	daily physiological calculations, with carbon allocation to growth calculated annually (or as specified by user)
Mortality sources	? individual trees are not simulated. No mortality sources are described in Running and Gower 1991 or in the base model description in Running and Coughlan 1988.
Sub-lethal stresses	? as for mortality sources
Measure of stress	? as for mortality sources
Soil scale	models available nitrogen pool and "water stress"
Atmospheric scale	base model considers temperature and precipitation in physiological calculations
Nutrients	nitrogen and water
GPP calculation	see base model description (Running and Coughlan 1988)
Interactions	
Carbon allocation	intention is to i) calculate the maximum carbon that can be put into leaf production given the availability of photosynthate, nitrogen and water; and then ii) allocate the remaining carbon first to root growth in proportion to leaf growth, and finally to stem growth. The proposed numerical methods are unclear due to problems in the published model description. Consideration of equations 5, 6 and 7 in Running and Gower 1991 suggests that stem growth must always be negative (i.e. use equation 6 to substitute for C_R in equation 7, and then use equation 5 to substitute for C_L in the resulting equation). Equation 3 shows that nitrogen can never be limiting if one hectare of soil contains more nitrogen than one kilogram of leaves. Equation 3 also has the result that the maximum carbon available for leaf production has units of square kilograms per square hectare per year. The variable $R_{L/R}$ appears to be used inconsistently as both the ratio of leaf to root C allocation, and the proportion of <i>total</i> C allocated to leaves.

Model	Kellomäki et al. 1993 'FINNFOR'
Summary	A very detail object-oriented model designed to assess the effects of climate change on the structure and functioning of boreal forests
Calibration	boreal coniferous forests
Vegetation scale	tree cohorts are followed within each stand. Each cohort is characterized by species, age, diameter, "length", seed crop production, crown (by foliage age classes), branches (by heartwood, sapwood, etc), fine and coarse roots (by heartwood, sapwood, etc), stem, leaf area index, root depth, growing season and daily frost resistance.
Spatial representation	stands are located at explicit coordinates across whole regions. Each stand/coordinate-position is characterized by species present, diameter distribution, climatic variables and soil conditions.
Time step	hourly, through seasons up to centuries. Growth, recruitment and death processes are all modeled.
Mortality sources	represented by cohort-specific annual death rates
Sub-lethal stresses	frost
Measure of stress	frost resistance is calculated for each cohort, and influences foliage damage
Soil scale	models organic layer, litter, humus, inorganic soil and ground water table. Water and heat flow through soil, and snow properties are treated in detail.
Atmospheric scale	models temperature, precipitation, CO ₂ concentration, wind and cloud cover
Nutrients	considers Ca, K, Mg, N, and P. For litter and humus, calculates N mobilization and N/C ratio.
GPP calculation	modeled details include stomatal conductance (calculated from temperature and vapor pressure data), crown shadows and gaps, shading from other cohorts ...
Interactions	many?
Carbon allocation	depends on cohort-specific allocation factors for each component. These appear to be constant for each cohort. See pg. 80 and 82.

Model	Rastetter and Shaver 1992
Summary	Designed to explore single vs. multiple element nutrient limitation. Nutrient uptake rate depends on biomass to the 2/3 power, to approximate surface area effect. Total element uptake per unit surface area is limited, but the plants can "acclimate" by re-allocating the total uptake rate between two different elements.
Calibration	none (abstract model)
Vegetation scale	models average characteristics of an area of uniform, monospecific vegetation
Spatial representation	none
Time step	abstract time units
Mortality sources	none
Sub-lethal stresses	nutrient availability
Measure of stress	none
Soil scale	effects of soil and air quality are only represented in the "element replenishment rate" and "rate of element loss from vegetation"
Atmospheric scale	as for soil, above
Nutrients	two abstract nutrients are considered
GPP calculation	none - plant biomass is taken to be the sum of the "concentrations" of the two elements in plant biomass (p. 1158)
Interactions	either or both elements may be limiting
Carbon allocation	none

Model	Cropper and Gholz 1993 'SPM'
Summary	designed to simulate carbon dynamics through the growing season, for comparison to measured values
Calibration	Florida slash pine on a plantation in northern Florida
Vegetation scale	models stand averages of new and old foliage, stem, branches, fine and coarse roots in litter, and fine roots in mineral soil
Spatial representation	none
Time step	hourly physiological calculations and daily biomass adjustments, through one annual cycle (or longer, but only after canopy closure at age 14)
Mortality sources	none
Sub-lethal stresses	only the balance of carbon between assimilation and respiration. Assimilation rates do not depend on water availability.
Measure of stress	none
Soil scale	models dead fine roots, needle litter, and soil organic carbon
Atmospheric scale	considers hourly temperature
Nutrients	none (the model correctly predicts increased growth on fertilized sites, but this appears to be because a larger initial leaf area is input for these sites; see page 243)
GPP calculation	depends on foliage area and efficiency, and is calculated separately for old and new foliage, taking into account their different vertical distributions
Interactions	none
Carbon allocation	new needle growth has first priority, and occurs whenever a threshold value of "labile carbon" is present, even when daily NPP is negative. Other growth occurs only when NPP is positive. Allocation to each tree component depends on partitioning coefficients. The authors consider this a "dynamic partitioning scheme", but the coefficients appear to be constant. See pg. 235.

Appendix 3: Potential IFTNC Carbon Allocation Analysis

1.0 Introduction

The Intermountain Forest Tree Nutrition Cooperative (IFTNC) has individual tree records for 572 fertilized and control plots going back 1980. One goal of the fertilizer trials was to be better able to predict tree response to fertilization. Existing growth and yield models have so far been unable to account for the observed, aboveground, growth responses. This may be because fertilized trees allocate a different proportion of their resources to belowground growth than do unfertilized trees, a possibility which is not adequately represented in the existing models. The following sections describe a potential analysis to examine the IFTNC data for evidence that belowground allocation is different on the fertilized plots than on untreated control plots.

2.0 Overview of Analysis

Belowground allocation is notoriously difficult to measure. To overcome this difficulty, the analysis would take advantage of the fact that belowground carbon allocation must be equal to the difference between total photosynthate production and aboveground carbon allocation. The general idea is to use one of the sophisticated simulation models that are available to predict total annual photosynthesis and aboveground respiration on each plot, and to then subtract the observed aboveground growth. The proportion of carbon allocated belowground could then be compared across fertilized and control plots, and related to the measured resource availability and time since treatment on those plots. Table 1 illustrates the analysis. Note that the simulation model would be run for only one year at a time, so that the actual, observed initial conditions could be input at the beginning of each year (rather than allowing the model to grow trees using its own assumptions about carbon allocation, which could introduce progressively larger errors in the estimated production for each year).

Table 1. *Analysis: Does percent allocation belowground change with resource availability?*

Plot	Year	Treatment	Nitrogen Availability Index	Estimated Total Photosynthesis {A}	Aboveground Allocation:		Belowground Allocation:	
					Estimated Respiration {B}	Total Growth {C}	Total Allocation {D=A-(B+C)}	Percent Allocation {100*D/A}
1	1980	-						
	1981	+ 200 lbs N						
	1982	-						
	1983	-						
	...	-						
2	1980	-						
	1981	+ 400 lbs N						
	1982	-						
	...	...						

3.0 Data Requirements of Analysis

As described in the previous section, a simulation model would be used to generate estimates of total photosynthesis and aboveground respiration on each plot. One possibility is to use a new version of the ForestBGC model (Running and Coughlan 1988, Running and Gower 1991) that has improved photosynthesis algorithms (Ronni Korol, pers. comm.). This model has two main advantages for the project: the photosynthesis routines have been recently revised and parameterized (Ronni Korol, pers. comm.) for the region of some of the plots; and nearly-suitable climate files have already been compiled because an older version of the model was used to estimate the productivity of some of the IFTNC plots (IFTNC Twelfth Annual Report, part 3).

ForestBGC (BGC) has many input requirements. The inputs which will affect the model's estimates of photosynthesis and respiration in the first year of simulation, and are therefore most critical to this analysis, include the following: climatic data; initial Leaf Area Index (LAI; total, not projected, in m^2/ha); the initial mass of carbon in both living and dead stemwood, leaf, and root pools (kg/ha); the leaf nitrogen concentration; parameters to define the dependence of stomatal conductance on temperature, vapor pressure deficit, leaf water potential, etc; parameters to describe the timing of fine root and leaf production and loss; and parameters to specify leaf, stem and root maintenance respiration rates and growth respiration proportions. Of these input requirements, LAI and leaf nitrogen have the strongest influence on the estimates of photosynthetic production (Running and Coughlan 1988; Ronni Korol, pers. com). The estimation of aboveground respiration will be affected by most of the input data.

The rest of this section describes how these input data requirements may be met. It also describes the calculation of aboveground growth, and considers the likely influence of each estimate on the results of the analysis.

3.1 Climatic Data

When Peter Mika ran BGC for some of the IFTNC sites, he used available data climate station data, linear regression, extrapolation and the MTCLIM model to develop BGC climatic data files for an "average composite year" (IFTNC Twelfth Annual Report, part 3). These files are available for 33 sites in north and central Idaho. The analysis could be limited to these sites.

Refinements to BGC since Peter's work with the model mean that the climatic data files must now include daylength (Ronni Korol, pers. com). Peter Mika already has this calculated for the sites that he studied, so it can be added to the files.

potential influence of uncertainty

"Random" errors in the estimation of average annual climate for each site will not bias the analysis¹ as these errors are expected to average out between the 64 different sites. If, however, the predicted average annual climate differed systematically from the actual climate at each site (for example, because the years at the time of the fertilizer trial were hotter or wetter than usual during the period on which the composite was based (1965 to 1988), or because of a systematic error in the climate estimation process), then this error could affect the analysis.

For example, using an average year that is too cloudy (i.e. shortwave flux density is too low) will cause BGC to underestimate total photosynthesis, and underestimate it more on the plots with the greatest leaf area index. Since the plots with the greatest leaf area are expected to be the fertilized plots, this means that production will be underestimated more on fertilized plots. This will make it look as though less carbon was allocated belowground

¹ By increasing the variation, however, random errors could make it less likely that the results will be significant.

than would be expected in proportion to aboveground growth, a result which favors the dynamic-allocation hypothesis. Errors in other directions could favor the null hypothesis. Because the direction of these effects cannot be known in advance, we may consider them “unbiased on average”. Any source of error would only be of concern if it underestimated photosynthesis *in proportion to respiration* more on treatment plots than on control plots, or overestimated respiration in proportion to photosynthesis more on treatment plots.

The potential for errors of this sort can be reduced by verifying that the weather during the time between fertilizer application and the focal year(s) of the analysis was similar to the longer-term average (which was based on the years 1965-1988).

Conclusion: probably no net bias.

3.2 Initial Leaf Carbon and LAI

Estimating leaf carbon or leaf area may be the most difficult step in the analysis. According to Peter Mika, the IFTNC has no data on leaf area or light attenuation through the canopy at the fertilizer installations. John Marshall has a student doing water allocation work, who will be doing leaf area measurements as part of this work. However, we are most interested in leaf area nearer to the time of fertilizer applications (1981/82 and 1987/88).

Two options are available for estimating leaf area. One method is to use a regression based on sapwood area and/or dbh. The regression could be used to estimate the leaf area of each tree on a sample plot. Summing the estimated leaf areas of each tree and dividing by the plot area would then give the LAI of the site. The IFTNC has available sapwood measures for one point in time on the control plots (Peter Mika, pers comm). To estimate leaf area on the fertilized plots, a regression based on dbh could be used, although some authors consider this to be a less accurate relationship (e.g. Grier and Waring 1974, Snell and Brown 1978, but not Brix and Mitchell 1983; all authors considered Douglas-fir trees). Peter Mika used published equations for LAI as a function of sapwood area and dbh ten years ago, and was “very unhappy” with the resulting numbers. Moreover, the relationship between sapwood area and LAI has been shown to change under fertilization (Brix and Mitchell 1983, studying coastal Douglas-fir).

The other option (Kurz 1989a) for estimating LAI requires knowing the location and size of all the neighbors of a focal tree that is destructively sampled to determine its actual leaf area. A regression can then be used to determine the relationship between the focal tree’s size, the size and proximity of its neighbors (Crown Competition Factor), and its leaf area. The resulting equation is available for coastal Douglas-fir (Kurz 1989a). However, this methodology could not be applied to interior Douglas-fir at the IFTNC sites as no foliage biomass measurements are available for any sample trees and nor are any stem location data available. This means that the sapwood area / dbh regressions are the best option for estimating leaf area at the IFTNC sites.

For some purposes, such as the estimation of respiration, BGC considers the kg C / ha in the leaf pool rather than LAI. The model converts leaf area and leaf mass by means of the “Specific Leaf Area” (SLA; area per unit weight in m²/kg), which is a user-input constant in the model. Unfortunately, the IFTNC does not have data on the relationship between leaf area and biomass on any of their plots (Peter Mika, pers comm). SLA will therefore have to be estimated from other sources, either as a single, constant value or as a relationship based on fertilizer application, annual radiation input, or other variables.

potential influence of uncertainty

Fertilized trees are known to have more foliage for a given sapwood area than do unfertilized trees. This means that using a constant sapwood:leaf area relationship developed from the control plots or taken from the literature is likely to underestimate total LAI - and therefore total photosynthetic production - on the fertilized plots. This

will make it look like less carbon was allocated belowground than was actually the case, a result which favors the hypothesis of dynamic allocation.

The estimation of SLA has the potential to introduce additional errors into the analysis. We need to determine whether SLA changes under different fertilizer treatments. Errors in the estimation of SLA could affect the results of the analysis in either direction, as was discussed above for climatic data.

Conclusion: Unless a dbh-foliage relationship can be found that is specific to fertilized trees, the analysis will be biased in favor of the dynamic-allocation hypothesis.

3.3 Initial Stem Carbon

The volume of stem wood will be calculated from the average height and dbh observed on each plot using standard taper equations (taken from FVS, and already attached to Peter Mika's plot data files). Stem wood density data will then be needed to convert the calculated wood volume to kg C / ha for BGC.

potential influence of uncertainty

The taper equations in FVS have been extensively researched and validated, so should not be a source of error in the analysis. As long as fertilized trees may be presumed to grow according to the same taper relationships as unfertilized trees, the standard equations can be applied to both control and treatment plots. The IFTNC has tree taper data for 823 trees at 90 sites, so it should be possible to test for ourselves whether taper relationships depend on treatment, if necessary.

The only complication is that there is also some work showing that fertilized trees produce less dense wood (more low density spring wood; Peter Mika, pers comm.). To ensure that the test of dynamic allocation is conservative, one should be sure to err on the side of underestimating aboveground allocation on fertilized plots. Since BGC will be run only for single years in this analysis, the stem carbon pool may affect only estimated maintenance respiration. To ensure that this quantity is underestimated, the weight of stem carbon on fertilized plots should be underestimated rather than overestimated. If no better data are available, this may mean assuming that *all* of the observed post-treatment increase in growth on fertilized plots is low-density spring wood. Springwood is 60 - 70% less dense than winter wood.

Conclusion: If necessary, the possible bias can be avoided by assuming that all of the increase in growth on fertilized plots is low-density wood.

3.4 Initial Root Carbon

Although the model also simulates a root carbon pool, root carbon should not influence BGC's photosynthate and aboveground respiration estimates in the first year of the simulation. Subsequent years would be affected as the model attempted to simulate changes in leaf nitrogen, but, as noted above, the intention is to re-start the model for every year for which data is desired in order to input the actual observed stand conditions.

For purposes of initializing the model, root carbon can be estimated by any "standard" regression on dbh. Root carbon could simply be assumed to equal about 23% of the total aboveground biomass (Kurz et al. 1996).

potential influence of uncertainty

Conclusion: errors in estimating root carbon have no influence on BGC's estimation of total photosynthetic production or aboveground respiration in the first year of simulation, and therefore have no influence on the results of our analysis.

3.5 Leaf Nitrogen Concentration

Leaf nitrogen concentration data (two trees per plot, from the “buffer zone”) at one year after fertilizer applications are available for all of the IFTNC sites (Peter Mika, pers comm). To analyze growth during the first year after application, one could either use the same leaf nitrogen values as observed at the end of that year, or apply the values for the control plots to all plots (see below). For subsequent years, the observed values might be applied as if they held constant.

potential influence of uncertainty

The analysis results for the second season after fertilizer application will be of most interest because actual leaf nitrogen concentration is known for this year. If one assumes that fertilized trees maintain the same leaf nitrogen in subsequent years, then leaf nitrogen on the treatment plots is likely to be over-estimated at some time in the future (because soil nitrogen availability will decline in subsequent post-treatment years, and – if the dynamic allocation hypothesis is correct – there will be fewer roots per unit foliage to take up the remaining nitrogen in subsequent years). However, over-estimating leaf nitrogen in BGC will result in total photosynthesis being overestimated. Since observed aboveground production and predicted aboveground respiration will not be affected, the net result will be that we overestimate belowground allocation on the treatment plots. This error favors the null hypothesis (static carbon allocation), and will lead to a conservative test. This argument suggests that one should also use the higher, fertilized leaf nitrogen measurements for the first year after treatment (not the control measurements).

Conclusion: Leaf nitrogen will not be a source of error in the second year after treatment. In subsequent years, the estimation of leaf nitrogen will be a source of error that acts against the dynamic allocation hypothesis.

3.6 Other Input Requirements

[suitable parameters to fill the other input requirements are assumed to be available]

potential influence of uncertainty

Some of the parameters, for example, aboveground maintenance and growth respiration rates, are obviously critical to our analysis. Possibly, these values should differ between control and treatment plots. Other parameters, for example, the day of leaf production and loss, could influence the analysis in the same way as could the climatic data discussed in Section 3.1: the errors are unknown and could be in either direction. Still others, such as the soil nitrogen parameters, should not affect the results of the first year of simulation at all.

Conclusion: With so many parameters, any biases attributable to individual parameters should tend to average out.

3.7 Aboveground Growth

The analysis would consider only the increase in stemwood volume, which would be calculated as the difference between the volume calculated from the observed dbh and height at the beginning of the year, and those observed at the end of the year. Taper relationships were discussed in Section 3.3.

4.0 Conclusions

Care should be taken to use the best available data in meeting BGC's input requirements. The main concern is the method by which LAI will be estimated. In spite of this concern, if the results of the analysis are positive, they will support the argument that the issue of dynamic allocation merits more attention.

5.0 Analysis Steps

The first step in the described analysis would be to locate and obtain access to a forest growth model that can project total growth (aboveground and belowground combined) in response to changes in soil N availability. Assuming that ForestBGC or something like it were to be adopted for use in the analysis, the next steps in completing the analysis would be as listed below. This list was developed during a conference call between Al Stage, Ronni Korol, Peter Mika, Werner Kurz and Julee Greenough on August 9, 1995.

- Illustrate initial fluctuation in BGC results as input LAI adjusts to site water balance.
- Show default input parameters and output format.
- Describe required soil texture data.
- Suggest references for wood density, etc.
- Specify which site is to be omitted due to lack of nitrogen data.
- Describe desired output.
- Make final decision on which version of BGC to use, whether to use dynamic or static allocation, and whether multi-year run is needed to stabilize leaf mass.
- Provide leaf nitrogen data for each plot.
- Extrapolate leaf nitrogen data between years.
- Add daylength to climatic data files.
- Provide soil texture data.
- Locate a suitable relationship between sapwood area and dbh, and estimate LAI on each plot in each year.
- Find a suitable estimate of SLA.
- Calculate initial stem carbon for each plot in each year.
- Calculate initial root carbon for each plot in each year.
- Obtain other input parameters required by BGC.
- Do BGC runs.
- Test for change in belowground allocation.